

RAEMEOTHERIUM YATKOLAI, gen. et sp. nov.,
A PRIMITIVE DIPROTODONTID FROM THE MEDIAL MIOCENE
OF SOUTH AUSTRALIA

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Abstract

A new genus and species, *Raemeotherium yatkolai*, from the medial Miocene Namba Formation in South Australia, is the most primitive member of the Diprotodontidae yet described. On its most anterior lower molar is a well-developed paracristid and protocristid. This, together with a strong cristid obliqua on all lower molars suggests derivation of diprotodontids from selenodont rather than quadritubercular ancestors.

Introduction

In September 1976, Mr Ian Stewart (National Museum of Victoria) discovered the diprotodontid dentary here described as *Raemeotherium yatkolai* (SAM P19764). It was found at the south end of Lake Pinpa, South Australia, in the medial Miocene Namba Formation. Only one or two centimetres away at the same level was a mandible of a species of pseudocheirine similar generically to that Tedford *et al.* (1976, p. 56) characterized as '... the most abundant mammal in the Pinpa Fauna . . .', (NMV P48616, see pl. 16, fig. 10).

Three additional isolated teeth referred to *Raemeotherium yatkolai* were collected ten kilometres to the south on the west side of Lake Namba at a site in the Namba Formation designated as South Prospect B by Woodburne and Tedford (1975). A single isolated upper incisor of *R. yatkolai* was found at Ericmas Quarry, four kilometres to the north on the west side of the same lake, again in the Namba Formation.

Callen and Tedford (1976, p. 135) and Tedford *et al.* (1977, pp. 56-57) discuss the basis for assigning a medial Miocene age to the Namba Formation.

Abbreviations

AM Australian Museum, Sydney.
AMNH American Museum of Natural History, New York.
BMNH British Museum (Natural History), London.

NMV National Museum of Victoria, Melbourne.
SAM South Australian Museum, Adelaide.

Terminology and Measurements

Mandibular terminology follows Stirton (1967), dental terminology is modified from Archer (1976) (see fig. 1), and enumeration of the teeth follows Archer (in press) (see fig. 1, 2). The system of tooth enumeration used here departs radically from all previously proposed. In it, the permanent cheek teeth of diprotodontids are P3, M2, M3, M4, M5. In contrast, in the two systems previously employed by Twentieth Century authors, the same teeth are designated P3 or P4, M1, M2, M3, M4.

Measurements were made with a Wild microscope equipped with a mechanical stage, enabling an accuracy of 0.1 millimetres.

Systematics

The following diagnoses are not intended to be exhaustive at each taxonomic level, but rather are restricted to those features which can be observed on the type and referred specimens of *Raemeotherium yatkolai*.

Class MAMMALIA Linnacus, 1758
Subclass THERIA Parker and Haswell, 1897
Infraclass METATHERIA Huxley, 1880

Supcrorder Marsupialia Illiger, 1811
Order Diprotodonta Owen, 1866
Family Diprotodontidae Gill, 1872

Diagnosis: Distinguished from all other Marsu-

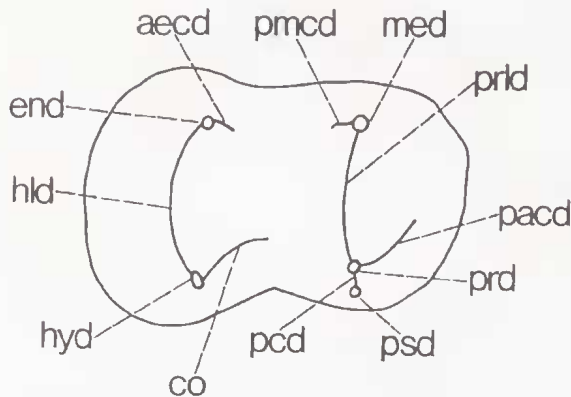


Figure 1—Schematic diagram of diprotodontid lower molar showing terminology employed. Abbreviations: aecd, anterior entocristid; co, cristid obliqua; end, entocoid; hld, hypoconid; hyd, hypoconid; med, metaconid; pacd, paracristid; pcd, protocristid; pmcd, posterior metaconid; prd, protoconid; prld, protolophid; psd, protostylid. Modified from Archer (1976).

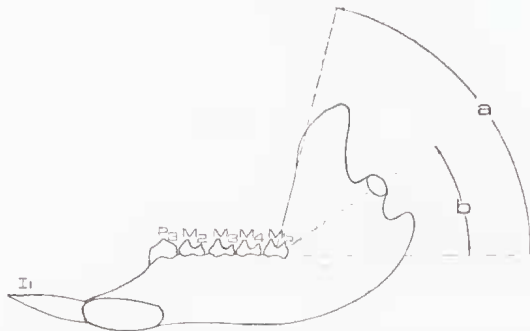


Figure 2—Schematic diagram of a diprotodontid mandible illustrating system of numbering teeth employed in this paper and method of measuring inclination of anterior border of ascending ramus (angle *a*) and elevation of condyle (angle *b*).

pialia by the presence of four simultaneously functional bilophodont molars lacking fore and midlinks and absence of a masseteric canal in the dentary.

Subfamily Zygomaturinac Stirton, Woodburne, and Plane 1967.

Diagnosis: Most members, including *Raemotherium yatkolai*, distinguished from all other diprotodontids by the presence of a distinct paracristid on M_2 .

Raemotherium gen. nov.

Type species: *Raemotherium yatkolai* sp. nov.

Known distribution: Medial Miocene, Tarkarooloo Basin, South Australia.

Diagnosis: Distinguished from all other diprotodontids by the presence of a distinct crest, the protocristid, directed buccally from the protoconid on M_2 ; a well-developed anterior entocristid on M_{2-5} ; and the ascending ramus more recumbent than in other species.

Etymology: RAEME, acronym for the Royal Australian Electrical and Mechanical Engineers; *θηριον*, Greek, beast.

Raemotherium yatkolai sp. nov.

Plate 16, figures 1-5, 7, 8, 11)

Holotype: SAM P19764, right dentary fragment with I_1 , M_{2-5} , and alveoli for P_3 . It lacks the P_3 , condyle, and angular region and has been crushed in a mediolateral direction so that traces of many structures on the medial side such as the digastric fossa have been obliterated.

Type locality and stratigraphic position: Namba Formation, southwest corner of Lake Pinpa, grid zone 6, grid reference 317146 on the Curnamona topographic series SH 54-14, 1: 250,000 (1965, South Australia), $31^\circ 8\frac{1}{2}'S$, $140^\circ 13'E$.

Diagnosis: That of the genus until other species are described.

Etymology: Named in honour of the late Mr Daniel A. Yatkola, a student of mammalian palaeontology.

Referred specimens: NMV P48537, isolated right M_4 or M_5 . NMV P48538, isolated right I^3 . AMNH 102186, isolated left M_4 . Collected from the Namba Formation, South Prospect B, Lake Namba, grid zone 6, grid reference 320135, Curnamona topographic series SH 54-14, 1:250,000 (1965, South Australia), $31^\circ 14'S$, $140^\circ 14'E$. They were found in the white coloured unit described by Woodburne and Tedford (1975, p. 3) as a ' . . . very fine sand . . .', developed as lenses within the ' . . . thin-bedded black claystone . . .', at South Prospect B.

AMNH 102183, isolated right I³. Collected from the Namba Formation, Ericmas Quarry, Lake Namba, grid zone 6, grid reference 320140, Curnamona topographic series SH 54-14, 1:250,000 (1965, South Australia), 31° 12'S., 140° 14'E. It was found in a channel deposit formed of white quartzose sand containing green limonite-cemented clayballs.

TABLE 1

Measurements (mm) of lower molars of
Raemeotherium yatkolai

	Length	Width Anterior Moieties	Width Posterior Moieties
SAM P19764			
M ₂	10.7	5.9	6.7
M ₃	11.0	6.5	7.4
M ₄	11.1	7.1	7.1
M ₅	11.2	7.2	7.0
NMV P48537			
M ₄ or M ₅	11.0	7.6	7.3
AMNH 102186			
M ₄ or M ₅	11.0	7.7	7.8

TABLE 2

Measurements (mm) of the mandible of
SAM P19764, type specimen of
Raemeotherium yatkolai

Length, diastema I ₁ -P ₃ : 15 ^a
Depth, horizontal ramus at anterior end of P ₃ : 19.0
Depth, horizontal ramus at middle of M ₂ : 25 ^a
Depth, horizontal ramus at middle of M ₄ : 26 ^a
Length, M ₂₋₅ : 44.2 ^a

^a = approximately.

Description

Mandible: The mandible is remarkably delicate compared with other diprotodontids and in this respect resembles those of similar-sized macropodids. The diastema between I₁ and P₃ is only about a third the length of the lower molar row. In outline, the symphysis is almost elliptical. Its major axis is about 25 mm in length and dips posteriorly at an angle of 35° with respect to the dorsal edge of the horizontal ramus. Its posterior edge is below the posterior root of P₃. The length of the minor axis is 13 mm. The surface of the symphysis is rough and there is no indication of its having been fused with the left mandible. The genial pit, for

the insertion of the geniohyoideus muscle, disrupts the outline of the symphysis at its posterior end as a notch of smooth bone. The mental foramen is located 1.7 mm anterior of the anterior edge of P₃, and 8.1 mm below the dorsal edge of the horizontal ramus. It is elliptical in outline with the major axis 4.2 mm in length and gently inclined anteriorly; the minor axis is 2.8 mm. Above and somewhat posterior to the mental foramen is a much smaller foramen. The ventral edge of the horizontal ramus below the molar row is gently convex downward. Posterior to that region, the shape of the ventral border is uncertain owing to crushing.

In the badly crushed posterior area of the mandible, part of the opening for the mandibular foramen is preserved 24 mm behind M₅ and about 3 mm below the level of the dorsal edge of the horizontal ramus. Distortion in this area is so great that the position in life of this foramen might have been several millimetres away. Despite the shattered nature of the posterior part of the mandible, there is no doubt that a masseteric canal was not present. The anterior edge of the ascending ramus is posteriorly inclined. Angle *a* as defined in Figure 2 is 62°. Although the condyle is not preserved on this specimen, because the dorsal part of the posterior edge of the coronoid process is intact, angle *b* as defined in Figure 2 could not have been more than 34°.

Lower dentition, I₁: The thin layer of enamel on this tooth is confined to the buccal and ventral surfaces above the alveolar border. Along the dorsal border of the enamel, a well-developed wear facet extends from the tip to about midway along the posterior edge of the enamel. An appression fossette is developed on the ventromedial surface of the enamel where this tooth contacted the left I₁. As on the molars behind, the enamel surface when unworn is wrinkled with gentle, irregular sinuous folds. The posterior end of the root is open and located beneath the middle of P₃.

P₃: This tooth is not preserved but its two alveoli are present in the type specimen. On the basis of the alveoli, this tooth, although much smaller, was similar to the P₃ of *Kolopsis torus*

in the ratio of its length to that of M_2 , and in the markedly greater posterior than anterior width.

M_2 : Unlike M_{3-5} , a distinct trigonid is developed on the anterior moiety of the M_2 . A well-developed paraclistid extends from the protoconid anterior to the forward margin of the tooth. A paraconid is not present at the anterior end of the paraclistid, but a cingulum begins at that point and extends posterolingually along the margin of the tooth, terminating at the anterior end of the swelling at the base of the metaconid. Part of the metaconid is missing but enough remains to confirm that the protolophid extends from the protoconid to the medial and slightly posteriorly positioned metaconid. A short ridge or cristid, the protocristid is directed posterobuccally from the tip of the protoconid. At the buccal end of the protocristid, there is a slight swelling to indicate the possible presence of a distinct cusp, the protostylid.

The cristid obliqua is directed anterolingually to abut against the posterior side of the trigonid at a point directly below and behind the protoconid. The hypoconid and entoconid are further apart from one another than the protoconid and metaconid. The hypolophid, connecting the hypoconid and entoconid, is convex posteriorly. A short anterior entocristid extends anterobuccally from the entoconid. Although present in other diprotodontids such as *Kolopsis torus*, this anterior entocristid is best developed in *Raemotherium yatkolai*. Along the posterior margin of the tooth is a well-developed, slightly crenulated postcingulum. Near the centre of the cingulum is a small cuspule. An extremely weak vertical ridge or prominent crenulation extends up the posterior slope of the hypolophid from this cuspule, and merges with the hypolophid wear facette. A definite wear facet extends the length of this ridge. The small cuspule is likewise truncated by a wear facet. None of the nearby crenulations display any significant degree of wear. Of the four principal cusps, the protoconid is the tallest and the other three (metaconid, hypoconid, and entoconid) are subequal in height. In occlusal view, the trigonid and transverse valley are subequal in

width and distinctly narrower than the talonid. M_{3-5} : The anterior moieties of these teeth are quite different from that of M_2 . In contrast, the posterior moieties of all molars are similar. A well-developed precingulum extends from the anterobuccal side of the protoconid base to the anterior side of the metaconid base. Unlike the M_2 , the paraclistid forms only a poorly defined vertical crest from the tip of the protoconid to its base, and because of this the anterior moiety is not distinctly triangular in outline when viewed from above. Between the protoconid and metaconid is a well-developed protolophid that is convex posteriorly in occlusal view. Projecting a short distance posterolingually from the tip of the metaconid is a small posterior metacristid. This structure is somewhat weaker on M_5 than on M_{3-4} . If it was present on M_2 , damage to that area of the tooth has removed all trace of the structure.

Because of the similarity in the posterior moiety of all lower molars, only differences from the condition of M_2 will be noted. The anterior entocristid becomes less-prominent posteriorly until on M_5 it has all but disappeared. The postcingulum is wider and extends further towards the lingual and buccal margins of the tooth than on M_2 . Cuspules are developed posterior and slightly buccal to the entoconid on the postcingulum. Only on M_3 however, is there a homologue of the ridge connecting the postcingulum with the crest of the hypolophid such as occurs on M_2 , and even here it is not as well-developed as it is on M_2 .

In order of decreasing height, the four principal cusps are the protoconid, metaconid, hypoconid, and entoconid.

TABLE 3
Measurements (mm) of I³s of
Raemotherium yatkolai

	Length	Width
NMV P48538	4.6	4.6
AMNH 102183	5.0	4.4

Upper dentition, I²: In occlusal view, this tooth has the outline of an isosceles right triangle, the corners of which are rounded, and the hypotenuse of which forms the posterolingual side. On the buccal side of the tooth is a broad, dor-

soventral groove and on the anterior side, a well-developed appression fossette resulting from contact with I². This tooth is quite similar in morphology to the homologous ones in *Ngapakaldia tedfordi*, *Neohelos tirarensis*, and *Plaisiodon centralis*.

Compared with measurements of *Ngapakaldia tedfordi* (Stirton 1967), *Kolopsis torus* (Woodburne 1967), and *Plaisiodon centralis* (Woodburne 1967), the I³s described here are about the proper size to correspond with the molars of *Raemeotherium yatkolai*. Because no other diprotodontids of this size are known from the Namba Formation and two referred molars of *R. yatkolai* were found in the same site and level as one of the two incisors (NMV P48538 at South Prospect B), we are confident that reference here to *R. yatkolai* is justified.

Discussion

Raemeotherium yatkolai is unique within the Diprotodontidae and the most primitive member in that the paracristid and protocristid are well-developed on M₂. The well-developed paracristid on M₂ is a feature of tribosphenic marsupials as well as some diprotodonts such as the selenodont possums. Archer (1976) suggested the possibility that lophodont marsupials (hence diprotodontids) may have been descended from selenodont or subselenodont possums. The well-developed paracristid on M₂, and the well-developed cristid obliqua on M₂₋₅ in *Raemeotherium yatkolai* at least suggest that diprotodontids did not descend from bunodont possums, but do not prohibit derivation from pre-selenodont tribosphenic ancestors, such as perameloids.

On the M₂ of selenodont diprotodonts buccal to the protoconid there is a variably-developed cusp that represents a protostylid; e.g. *Phascolarctos cineris* (NMV C2660, see pl. 16, fig. 9), and *Pseudocheirus peregrinus* (NMV C13937, see p. 16, fig. 6). On the M₂ of *Raemeotherium yatkolai*, the protocristid appears to have terminated in a protostylid (see pl. 16, fig. 7). Apparently the protostylid appeared as a neomorph on the M₂ of selenodont diprotodonts and their descendants secondarily reduced and then lost it independently in dif-

ferent lineages. Evidence for the presence of this cusp as the primitive condition in groups descendant from the selenodont diprotodonts is to be found not only in *R. yatkolai* in the case of the diprotodontids, but in an undescribed Miocene macropod as well.

Primitive diprotodontid features found in *Raemeotherium yatkolai* that are shared with some other members of the Diprotodontidae include the posteriorly inclined ascending ramus, the low position of the condyle on the dentary, all molars nearly the same size rather than markedly increasing in length and width posteriorly, and the well-developed anterior entocristid on M₂₋₅. Inclination of the ascending ramus is a quite variable feature within a given diprotodontid species. However, the recumbent angle (α in fig. 2) of *R. yatkolai*, 62°, is so much less than in any other diprotodontid that the differences can be confidently regarded as significant. *Kolopsis torus* with a minimum recumbent angle of 70° is the most similar diprotodontid, others fall in the range 80°-100°.

The ratio of M₂ to M₄ length typifies the difference between *Raemeotherium yatkolai* and other diprotodontids in molar lengths. In *R. yatkolai*, this ratio is 0.96, practically unity. The closest other diprotodontids are *Ngapakaldia tedfordi* where the ratio ranges from 0.78 to 0.89 in three specimens measured by Stirton (1967), 0.84 to 0.86 in three specimens of *Palorchestes painei* measured by Woodburne (1967), and 0.85 in one specimen (AM F44471) of *Kolopsis rotundus*. All other known diprotodontids in which this feature can be measured, have a ratio of less than 0.85. In the same manner, the degree of primitiveness of *R. yatkolai* in each of the remaining features listed in the preceding paragraph cannot be exceeded in another diprotodontid.

Some slight doubt remains as to whether *Raemeotherium yatkolai* is properly assigned to the Diprotodontidae because, as far as now known, the species has no derived or advanced character states which preclude its inclusion as a primitive member of the Macropodoidea. Although the presence of a masseteric canal, a derived condition within the Diprotodonta, is

a feature unique to macropodoids, the oldest member of the superfamily may well have lacked one. On the basis of parsimony, the last common ancestor of the macropodoids and their immediate sister-group, whatever that may have been, presumably lacked a masseteric canal, this lack being the primitive condition. This means that at the time of their separation, unless the masseteric canal appeared as a part of that particular speciation event, there would have been an ancestral macropodoid which lacked that structure. *R. yatkolai* could conceivably have been a descendant of such a primitive macropodoid or near-macropodoid. Hence allocation to the Diprotodontidae must be regarded as tentative although highly probable, pending discovery of better preserved specimens of *R. yatkolai*.

Assignment of *Raemeotherium yatkolai* to the Zygomaturinac within the Diprotodontidae must also be tentative because it is based on a primitive character state. By all the credible phylogenetic hypotheses that have been proposed for the Marsupialia, the presence of a strong paracristid on the M_2 is primitive within the diprotodontids. Hence, it is to be expected in the common ancestor of the family and could therefore be the condition in primitive, as yet unknown members of the other subfamilies. Discovery of a single P^3 of *R. yatkolai* would probably settle the matter because all the undoubted Zygomaturinae share a unique derived morphology of that tooth.

Only one diprotodontid specimen is significantly older than *Raemeotherium yatkolai*. This is a form tentatively regarded as a palorchestine by Tedford *et al.* (1975) who reported its presence in the late Oligocene or older Geilston Bay local fauna collected near Hobart, Tasmania. Unfortunately, this specimen (BMNH 40157) is not directly comparable with any known material of *R. yatkolai*, being a maxilla with part of M^2 and M^{3-5} . However, the lengths of the respective tooth rows indicate that these two diprotodontids are about the same size and the smallest members of the family. They likewise show molars of similar length without conspicuous backward increase in size typical of later diprotodontids.

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same agency and grant in 1973 when he re-visited the area and discovered the first referred specimens.

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Mr. Frank Coffa took the photographs and Mr. Alex Jelowyi did the lettering for the plate, Miss Jeanette Cook drew fig. 1 and Mr Harley Veitch, fig. 2.

Explanation of Plate 16

Raemeotherium yatkolai. SAM P19764, type, right mandible, Lake Pinpa, South Australia, fig. 4, lateral

view, x1; fig. 5, medial view, x1; fig. 7, occlusal view of M_{2-5} , x2; fig. 11, occlusal view x1. NMV P48537, isolated right M_4 or M_5 , South Prospect B, Lake Namba, South Australia, fig. 1, occlusal view, x2. AMNH 102186, isolated left M_4 or M_5 , South Prospect B, Lake Namba, South Australia, fig. 2, occlusal view, x2. NMV P48538, isolated right I^3 , South Prospect B, Lake Namba, South Australia, fig. 3, occlusal view; fig. 8, lateral view, all x2.

Pseudocheirine, NMV P48616, right mandible, found one or two centimetres from type specimen of *Raemeotherium yatkolai*, Lake Pinpa, South Australia, fig. 10, occlusal view, x4.

Pseudocheirus peregrinus, NMV C13937, left mandible, juvenile, fig. 6, occlusal view of M_{2-3} , x4.

Phascolarctos cinereus, NMV C2660, left mandible, juvenile, fig. 9, occlusal view of P_3-M_3 , x2.

Abbreviations: med, metaconid; prd, protoconid; psd, protostylid.